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Landscape-scale analyses suggest both nutrient and antipredator advantages to Serengeti herbivore hotspots

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Abstract. Mechanistic explanations of herbivore spatial distribution have focused largely on either resource-related (bottom-up) or predation-related (top-down) factors. We studied direct and indirect influences on the spatial distributions of Serengeti herbivore hotspots, defined as temporally stable areas inhabited by mixed herds of resident grazers. Remote sensing and variation in landscape features were first used to create a map of the spatial distribution of hotspots, which was tested for accuracy against an independent data set of herbivore observations. Subsequently, we applied structural equation modeling to data on soil fertility and plant quality and quantity across a range of sites. We found that hotspots in Serengeti occur in areas that are relatively flat and located away from rivers, sites where ungulates are less susceptible to predation. Further, hotspots tend to occur in areas where hydrology and rainfall create conditions of relatively low-standing plant biomass, which, coupled with grazing, increases forage quality while decreasing predation risk. Low-standing biomass and higher leaf concentrations of N, Na, and Mg were strong direct predictors of hotspot occurrence. Soil fertility had indirect effects on hotspot occurrence by promoting leaf Na and Mg. The results indicate that landscape features contribute in direct and indirect ways to influence the spatial distribution of hotspots and that the best models incorporated both resource- and predation-related factors. Our study highlights the collective and simultaneous role of bottom-up and top-down factors in determining ungulate spatial distributions.

Key words: forage quantity vs. quality; grazing lawns; herbivore habitat selection; near-infrared difference vegetation index (NDVI); predator–prey; remote sensing; Serengeti; soil nutrients; structural equation modeling; topographic relief; ungulate spatial distribution.

Introduction

The discussion of top-down vs. bottom-up factors in the regulation of mammalian herbivore populations has been prominent in ecology for over 50 years (e.g., Binkley et al. 2006) and remains a compelling research topic today (Sinclair 2003, Ripple and Beschta 2004, Festa-Bianchet et al. 2006, Wang et al. 2009; Hopcraft et al., *in press*). Both predation risk and nutrient or energy maximization have been identified as key features that determine the spatial distribution of ungulate habitat selection (Jarman 1974, Wilmshurst et al. 2000, Sinclair et al. 2003, Fryxell et al. 2004, Creel et al. 2005, Owen-Smith 2008). One challenge has been to determine the relative importance of forage attributes (e.g., quantity and quality) vs. predator avoidance in determining ungulate habitat selection (Bleich 1999, Kie 1999, Pierce et al. 2004). Resource- and predation-based mechanisms are not mutually exclusive, but rather operate simultaneously and interactively to influence herbivore distribution, abundance, and social organization (Jarman 1974, Sinclair and Arcese 1995, Wang et al. 2009).

Herbivore persistence depends upon access to relatively stable and predictable forage or relatively large areas that allow them to acquire forage despite environmental stochasticity (Fryxell et al. 2005). Furthermore, group vigilance (Fryxell et al. 2007) or predator-free refugia (Fortin et al. 2005, Mao et al. 2005, Valeix et al. 2009) reduce the impact of predation. As a result, suitable and persistent resident herbivore habitats should be those that combine these features in ways that optimize the net effects of forage quality and predation risk. One important, but often overlooked, feature of habitat selection by herbivores is that tradeoffs may exist among forage quantity, quality, and predation risk. For example, herbaceous biomass has a negative relationship with plant nutrient quality (Anderson et al. 2007*b*) and a positive relationship with predator cover (Riginos and Grace 2008). Such correlations make the identification of the precise mecha-

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nisms determining herbivore spatial distribution difficult to tease apart, and as a result, few studies have successfully separated the relative contribution of bottom-up and top-down factors.

The Serengeti ecosystem in East Africa is well-known for its migratory ungulate populations, one of the largest migrations of large herbivores on earth (Sinclair et al. 2008). Perhaps less appreciated are the local concentrations of intermixed resident herbivores that occur heterogeneously throughout the ecosystem. These resident areas, known as herbivore hotspots (McNaughton 1988, McNaughton and Banyikwa 1995), are composed of intermixed ungulate grazer assemblages and are temporally stable on the scale of several decades. That hotspots are, at least in part, maintained by resident ungulates themselves is an exciting and well-documented feature of their ecology (McNaughton 1988, McNaughton and Banyikwa 1995, McNaughton et al. 1997). Hotspots have elevated availability of key forage nutrients, but not inherently greater soil fertility (McNaughton 1988). In particular, plant Mg, Na, and P were identified as important because their availability met animal nutritional requirements within hotspots but fell below dietary needs in adjacent non-hotspot localities. Although predation has been identified as a key factor in the regulation of Serengeti herbivores (Sinclair et al. 2003), the influence of predation on the occurrence of hotspots remains untested.

In this study, we analyze mechanisms responsible for the spatial distribution of Serengeti hotspots, allowing us to address the hypothesis that both bottom-up and top-down factors simultaneously influence resident herbivore distributions. The specific objectives of our study were twofold: (1) to use remote sensing and GIS to spatially predict the distribution of hotspots across the Serengeti and (2) to investigate the ecological processes that determine the spatial distribution of hotspots, emphasizing resource- and predation-related factors. The first objective was achieved by using multiple logistic regression analysis of known hotspot sites to create maps of hotspot occurrence based on remotely sensed data across the ecosystem; predictions from the map of the best-fitting model were then tested against an independent data set on herbivore distribution. The second objective was achieved by sampling soil and vegetation characteristics at a subset of the sites and then using the data to test a hotspot process model using structural equation modeling (SEM). The mapping of stable resident hotspots provides future opportunities to address fundamental questions in large mammalian ungulate ecology, such as the importance of density dependence, temporal stability of resident home ranges, and the role of positive feedbacks in generating and maintaining resident habitats (Bolger et al. 2008).

Methods

Research was conducted in Serengeti National Park and three adjacent protected areas, Ikorongo, Grumeti, and Maswa, in Tanzania, East Africa (Fig. 1). These protected areas, along with Loliondo, Nogorongoro Conservation Area, and several protected areas in Kenya, are components of the larger 25 000-km^2 Serengeti–Mara ecosystem, hereafter referred to as Serengeti (Sinclair et al. 2008). Detailed descriptions of the geology, climate, and vegetation of Serengeti are provided elsewhere (Anderson et al. 2007*a*, 2008, Sinclair et al. 2008). Two related analyses were conducted: we used multiple logistic regression to create and validate a map of hotspot occurrence across Serengeti (part 1), and, in a separate analysis, we investigated specific mechanisms underlying the spatial distribution of hotspots at distinct sites using structural equation modeling (part 2).

Part 1: creation and validation of the hotspot map

Observations of herbivore abundance and distribution were conducted at 133 sites between February 2005 and May 2007 (Fig. 1). Sampling efforts were focused in regions with average rainfall >650 mm/yr (e.g., north and west of the Serengeti plains) because permanent hotspots do not generally occur below this threshold (McNaughton 1988, McNaughton and Banyikwa 1995). Sites were randomly chosen for sampling within stratified habitat types representing the dominant soil, vegetation, and climate zones in Serengeti; extreme or rare habitats, such as mountains, riverine forests, and kopjes were avoided. Sites were visited only in the wet season (February–May) to ensure that resident, rather than migratory, herbivores were observed. We focused our analysis on seven grazing ungulates characteristic of hotspots (McNaughton and Banyikwa 1995, hereafter referred to as "hotspot species"): zebra (*Equus burchelli*), wildebeest (*Connochaetes taurinus*), hartebeest (*Alcelaphus buselaphus*), topi (*Damaliscus korrigum*), warthog (*Phacochoerus africanus*), and gazelles (*Gazella* [*Eudorcas*] *thomsonii* and *G.* [*Nanger*] *granti*). At each site (~1000 m^2), ungulates were counted from a vehicle within a radius of 500 m and four 5-m^2 plots were randomly placed in which average herbaceous height and dung pellet groups were enumerated by species. Additionally, sites were photographed, inspected for herbivory, and assigned a categorical grazing intensity (0–5). Our point observations were supplemented by long-term animal monitoring conducted by the Tanzanian Wildlife Research Institute (TAWIRI) and Frankfurt Zoological Society (FZS) in order to establish a site as either a hotspot or non-hotspot (Appendix A).

Certain landscape or habitat features are often associated with increased predation risk, such as dense woodland patches, rivers, water holes, predator "viewsheds," and slopes (Hebblewhite et al. 2005, Hopcraft et al. 2005, Balme et al. 2007, Kauffman et al. 2007, Valeix et al. 2009). We focused on three landscape features we believed would predict the presence of hotspots, represent increased predation risk from the standpoint of a grazing herbivore, and could be quantified with

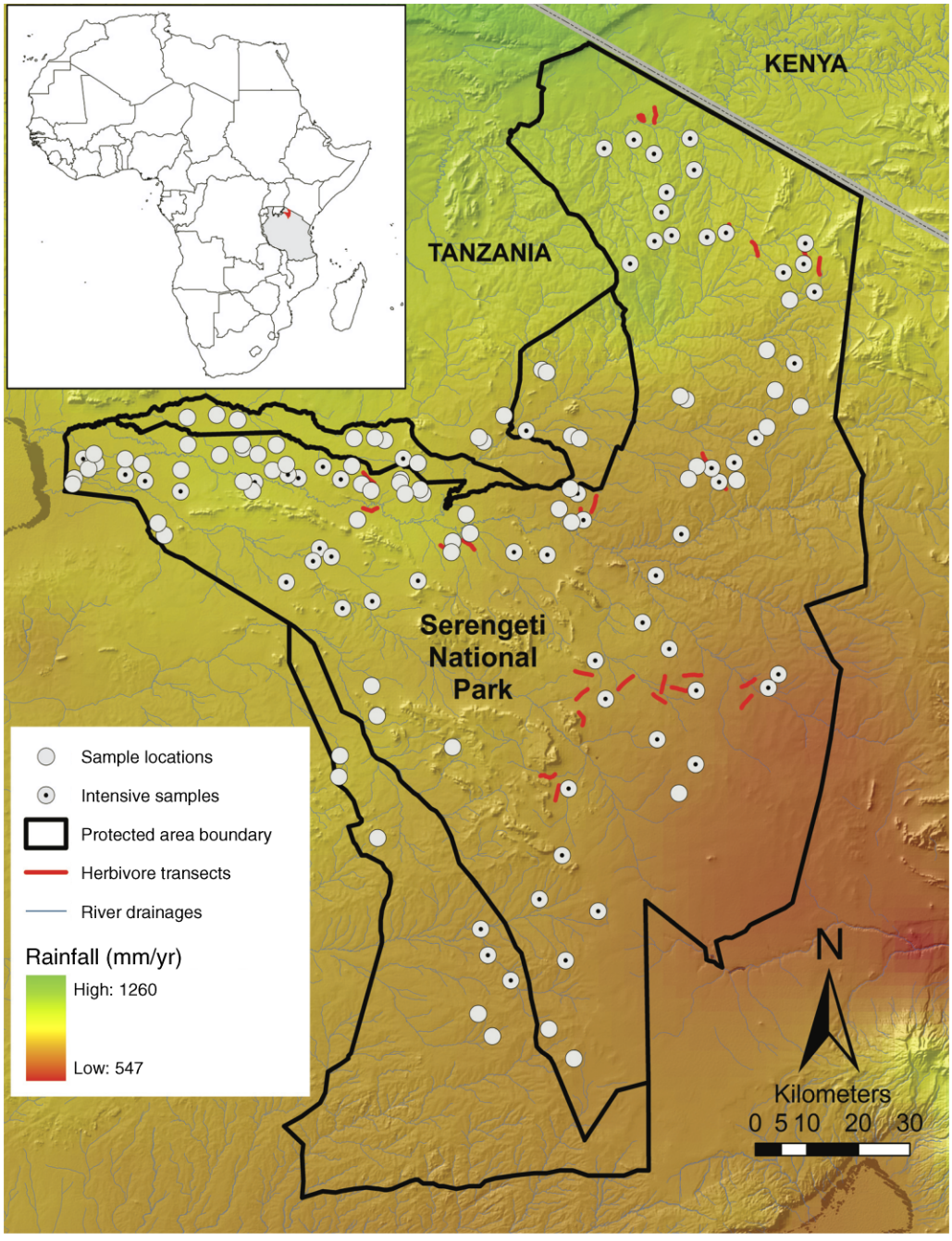

FIG. 1. Map of Serengeti National Park and protected areas (black lines) showing sampling locations (open circles), intensively sampled locations (open circles with black dots), and the herbivore transects (red lines). The map shows topographic relief, river drainages (blue lines), and mean annual rainfall (colored background). The inlay shows the location of the Serengeti (in red) on the border between Tanzania (shaded area) and Kenya.

remote sensing: landscape curvature, distance to nearest river, and topographic wetness index (TWI), which integrates watershed area and slope as a measure of moisture accumulation (Appendix A). River drainages and areas with high TWI values are often associated with woody vegetation, providing important cover for predators. Reanalysis of data from Hopcraft et al. (2005) demonstrates the association between these landscape features and the frequency of predation on hotspot ungulate species by Serengeti woodland lions (Appendix B) whose range occurs within our study area (Appendix E). Specifically, lions disproportionately killed prey near rivers and in areas of high TWI, while relatively flat areas were underutilized (Appendix B).

Additionally, as shorter, low-biomass grass swards are associated with energy maximization and higher nutrient forage quality (Wilmshurst et al. 2000, Fryxell et al. 2004, Anderson et al. 2007*b*), we hypothesized that the near-infrared difference vegetation index (NDVI) may predict hotspot occurrence by differentiating low- and high-biomass patches (Appendix A). However, because of the unpredictable and varying nature of the wet-to-dry-season transition in Serengeti, we restricted our analysis to two three-month periods: February–April (core wet season) and August–October (core dry season). Additionally, because we hypothesized that vegetation biomass and greenness would be relatively stable in hotspots over different seasons, we included the ratio of wet-season : dry-season NDVI. Mean annual rainfall was included as a predictor to understand the influence of climate on the presence of hotspots across Serengeti (Appendix A). Finally, because herbivores often track high-quality forage following fires (Archibald et al. 2005) and sustained grazing reduces fire (van Langevelde et al. 2003), we hypothesized that fire frequency might be either a positive or negative predictor of hotspots (Appendix A). Squared terms for fire, NDVI, and rainfall were included in the analysis to allow for nonlinear relationships between the environmental predictors and hotspot occurrence.

Assembly and selection of the best multiple logistic regression model was conducted in the generalized linear models (GLZ) module of STATISTICA version 8.0 (Statsoft, Tulsa, Oklahoma, USA) using the probit link and a binomial error distribution. The model-building options with best subsets based on Akaike information criterion (AIC) were used to identify the top six candidate models (MODEL1–MODEL6); these models represented the subset of environmental variables that best predicted the occurrence of hotspots across our 133 samples. Subsequently, the six models were used to create maps of hotspot occurrence at a spatial resolution of 250 m^2 for Serengeti National Park and the surrounding three game reserves in ArcGIS (Environmental Systems Research Institute, Redlands, California, USA). The models were then validated against independently collected herbivore transect data collected in March 2008 (Fig. 1). Twenty-six 3-km transects were established in which ungulates were counted from a slowly moving vehicle to a distance of 500 m on either side. Twelve 500-m^2 polygons, six on each side along the 3-km length, were created in ArcGIS for each transect and intersected with the six candidate hotspot probability maps. Each transect was then classified as a hotspot or not (Appendix A) and tested for accuracy against the six models using logistic regression with mean probability of hotspot occurrence from the maps as a predictor and classification of the transect (hotspot = 1, non-hotspot = 0) as the response variable. Additionally, to explore the relationship between hotspot occurrence and potential herbivore abundance, mean probability of hotspot occurrence for each transect was analyzed against the natural log of the number of herbivores counted on that transect using quantile regression with the "quantreg" package in R (R Foundation for Statistical Computing, Vienna, Austria).

Part 2: mechanistic analysis of processes at distinct sites

Because NDVI can represent the effects of multiple, correlated processes that may influence the presence of hotspots (e.g., biomass, forage quality, cover for predators, etc.), it was not used in the development of a mechanistic model. Instead, herbaceous vegetation quantity (in grams per square meter) and quality (leaf nutrient concentrations) were used as more direct measures of the fine-scale processes that may influence the spatial location of hotspots. Specifically, we focused on the availability of four nutrients, nitrogen (N), phosphorus (P), sodium (Na), and magnesium (Mg), because of their importance to herbivores in the system (Murray 1995, Anderson et al. 2007*b*) and their strong association with hotspots (McNaughton 1988). Intensive sampling was carried out at 66 of the previously described sites (Fig. 1; Appendix A) selected based on combinations of broad-scale soil and vegetation types (Herlocker 1976, Jager 1982). Soil fertility, measured as the sum of extractable base cations, was also quantified at the sites (Appendix A).

A conceptual model was created to represent theoretical relationships among climate (rainfall), landscape features associated with risk (curvature, distance to nearest river, and TWI), soil fertility, and vegetation quality and quantity, and their influences on the occurrence of hotspots (Fig. 2). The conceptual model provided a framework for the analysis of the data with structural equation modeling (Grace 2006; Appendix A) and assessment of the a priori hypotheses. Straight arrows in the diagram represent hypothetical causal influences of one variable on another, either positive (black lines) or negative (gray lines). In the context of the model, a direct path between landscape features and hotspots (Fig. 2, path A) suggests that their spatial distribution is influenced by structural variation in the environment associated with predation risk (curvature, distance from rivers, etc.).

In contrast, the influences of landscape features on hotspots may be indirect, mediated through landscape effects on resource quality and quantity (Fig. 2, paths B and C). An example is the influence of topographic variation on soil fertility and plant biomass in African savannas (Bell 1970, Anderson et al. 2006). The two main paths representing forage quality and quantity are those from plant nutrients (Fig. 2, path D) and plant biomass (Fig. 2, path E) to hotspots, both hypothesized to be positive. However, the path from plant biomass to hotspots represents two potentially contrasting processes in the model. First, as herbivores are often limited by forage quantity we hypothesized that hotspots would be associated with greater available biomass, once the negative effect of biomass on forage quality had been

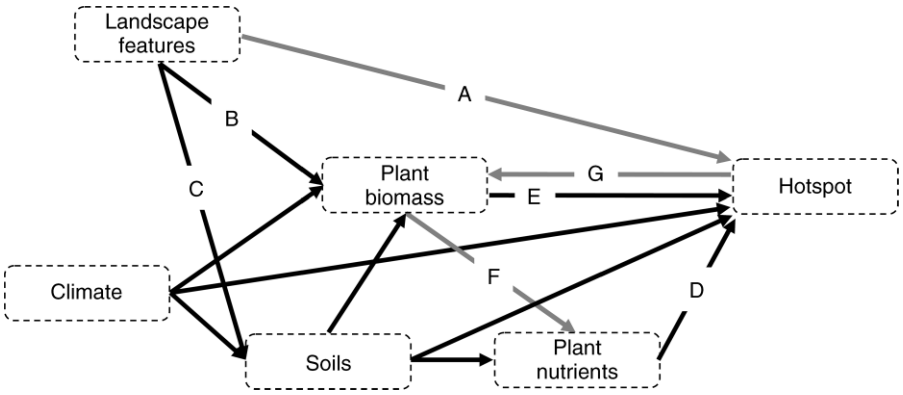

FIG. 2. The conceptual model used to guide the analysis of the observed data using structural equation modeling (SEM). Arrows show direct effects of one variable (dashed boxes) on another and were predicted to be either positive (black) or negative (gray). Letters represent specific mechanisms described in *Methods: Part 2: mechanistic analysis*.... The reciprocal effects between plant biomass and hotspots (paths E and G) represent a non-recursive interaction that can be tested for significance in SEM; see Grace (2006) for further information.

statistically controlled (Fig. 2, path F). In contrast, greater vegetation biomass provides more cover for predators and is associated with greater predator kill success (Hopcraft et al. 2005, Packer et al. 2005). Therefore, hotspots may instead be associated with lower biomass if hotspots provide better predator detection. Finally, should the only influence of biomass on hotspot presence be mediated through its effects on forage nutritive quality, then no remaining path between biomass and hotspot occurrence is expected. The relative strength and positive or negative sign of the path between biomass and hotspots will allow us to test these alterative hypotheses. As herbivores directly consume biomass an important potential feedback exists from hotspots to biomass (Fig. 2, path G), assumed to be negative with respect to standing plant biomass. However, there are many processes that cause variation in biomass across savannas (e.g., fires, soil fertility, soil water potential, etc.) and a nonsignificant path from hotspots to biomass suggests that not all sites with low biomass are hotspots (although all hotspots may have low biomass). Finally average annual rainfall (in millimeters per year) and soil fertility (Appendix A) were included to represent the major soil and climatic gradient across Serengeti.

RESULTS

Spatial distribution of Serengeti hotspots

Of the top six models (Appendix C), MODEL5, which included TWI, landscape curvature, distance to rivers, rainfall, dry-season NDVI, and wet-season : dry-season NDVI ratio, emerged as the best model predicting hotspot occurrence when tested against the independent transect data using logistic regression (AIC $= 24.99$, $\chi^2 = 7.1$, $P = 0.008$; Fig. 3A; Appendices C and D). Although the contribution of distance to rivers was only weakly supported by the multiple regression, the variable stayed in the model in a separate Bayesian probit analysis (Appendix D). MODEL5 also showed the strongest relationship between the 90% quantile of the number of grazing herbivores observed and the mean probability of hotspot occurrence (ln(herbivore count) $= 0.53 + 13.16 \times$ hotspot probability, $t = 3.49$, $P = 0.002$; Fig. 3B), suggesting that the map also provides a reasonable estimate of realized herbivore abundance. However, several transects had relatively high hotspot occurrence probabilities (>0.45) and few resident animals (Fig. 3B; Appendix E). More research may determine whether more available, but unoccupied, hotspot habitat exists in these low-rainfall areas or our map overpredicts hotspots in these areas.

Due to the dynamic nature of NDVI and rainfall, it is interesting, for heuristic purposes, to visualize where hotspots could potentially occur when only landscape features are considered. Toward this end, maps of the probability of hotspot occurrence are displayed as predicted by landscape factors only (Fig. 4A) and landscape plus climate factors (Fig. 4B). The difference between layers demonstrates that adding rainfall and NDVI to the analysis decreases the probability of hotspot occurrence across the majority of the landscape ([landscape only] $-$ ([landscape + climate layer] > 0 for 93% of the map pixels; Appendix E). However, that the probability of hotspot occurrence increases across $\sim$7% of the landscape by adding rainfall and NDVI to the analysis demonstrates that the imposition of dynamic variables cannot simply be seen as restricting the area of available habitat for residents from what would otherwise be suitable from the standpoint of risk. The areas in which hotspot probability was increased by adding dynamic variables are interesting because herbivores can influence the NDVI signal through consumption and can respond interactively to rainfall; indeed these areas matched up closely with the location of the hotspots (Appendix E). The model in the next section is designed to address mechanistic interactions among

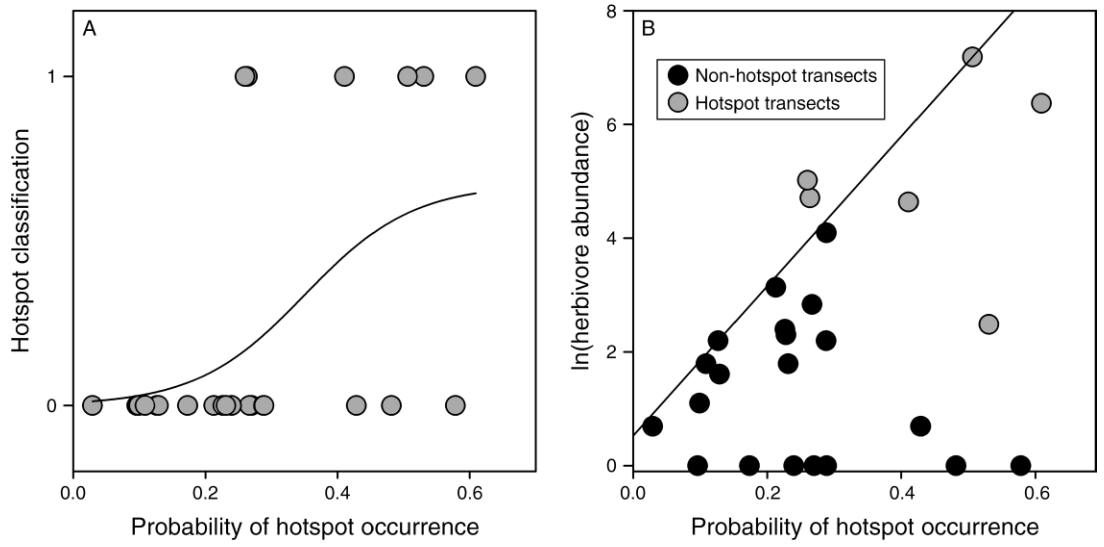

FIG. 3. (A) Probability of hotspot occurrence for MODEL5 vs. hotspot classification (0 = non-hotspot, 1 = hotspot) for 26 independent transects used to test the accuracy of the hotspot occurrence maps. The line shows the results of the logistic regression for MODEL5 (df = 24, deviance = 20.99, log likelihood = −10.5, $\chi^2 = 7.1$, $P = 0.008$). (B) Plot of the natural log of herbivores counted on a transect (Fig. 1) vs. the mean probability of hotspot occurrence for that transect resulting from MODEL5. The line depicts the upper 90% linear quantile regression (ln(herbivore count) = 0.53 + 13.16 × hotspot probability; SE of slope = 3.77, $t = 3.49$, $P = 0.002$).

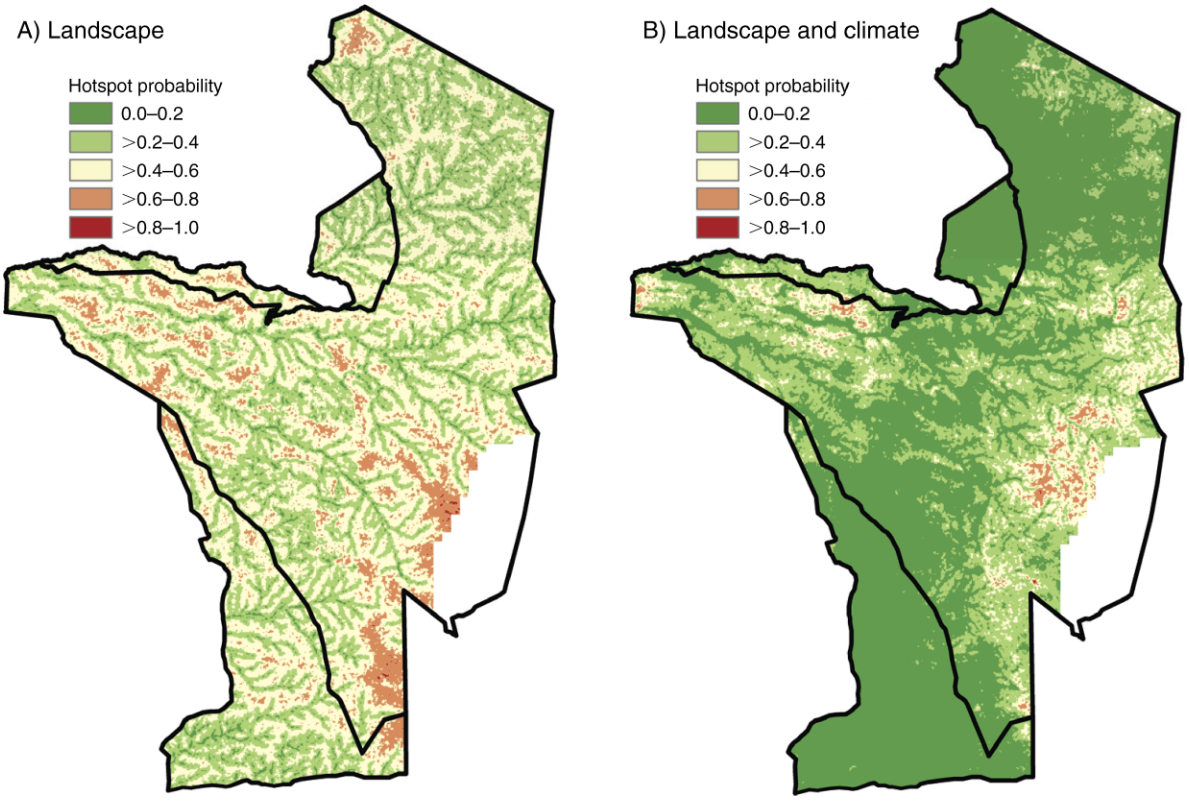

FIG. 4. Map results of MODEL5 showing the probability of hotspot occurrence based (A) only on landscape variables or (B) on landscape variables, rainfall, and near-infrared difference vegetation index (NDVI). Panel A is shown largely for heuristic purposes and represents hotspot probability based on static landscape features that represent predation risk, while panel B represents the addition of stochastic variables that, for the case of NDVI, may be partially influenced by herbivores.

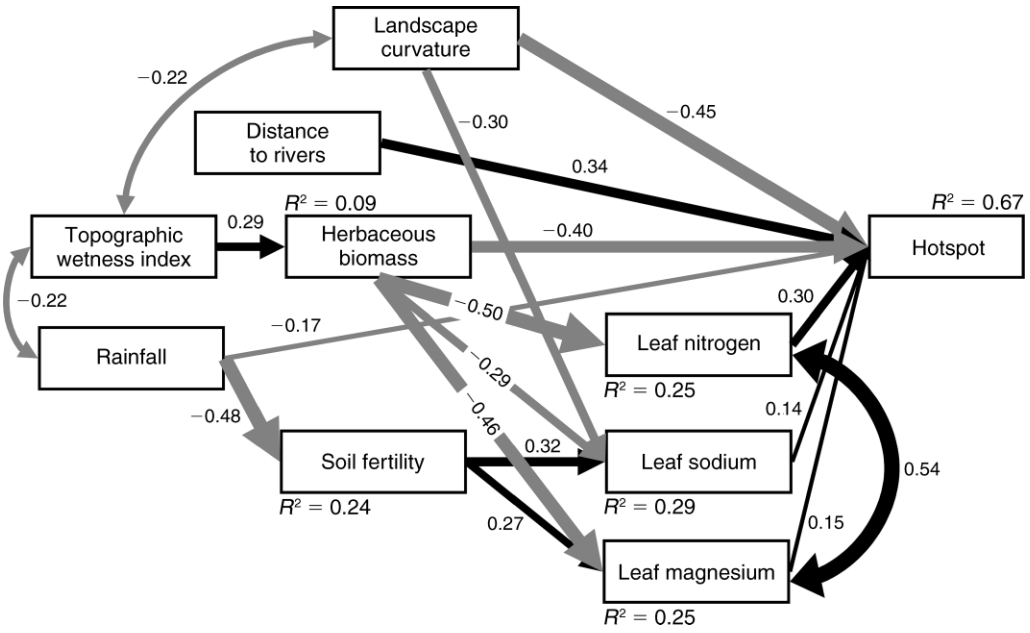

FIG. 5. Diagram showing the final structural equation modeling (SEM) results based on the analysis of 66 intensively sampled sites (Fig. 1; Appendix D), in which the occurrence of hotspots depended on landscape, climate, soils, and vegetation (Fig. 2). Straight arrows represent direct effects of one variable (boxes) on another, and curved arrows represent correlations; values associated with the arrows are standardized direct effects or correlations, with the arrow thickness proportional to the strength of standardized effects. Paths that included zero in their 95% credible range were omitted from the model (see *Methods*). For clarity, negative paths are shown in gray and positive paths are shown in black. The R^2 values adjacent to the boxes represent the total variance explained as a result of all predictors pointing to that variable. Total and indirect effects associated with the SEM results are reported in Appendix F.

climate, landscape variation, and forage quality and quantity more explicitly.

SEM results

The final structural equation model provided strong evidence that the observed data fit the a priori model (posterior predictive P value = 0.52) and explained ~67% of the variance in hotspot distribution across sites (Fig. 5). As expected, landscape curvature and distance to rivers both remained in the final model as significant direct predictors of hotspot distribution (flat areas away from rivers) and had standardized effects of −0.45 and 0.34, respectively (Fig. 5). The TWI, the other landscape feature, had only an indirect influence on hotspots through its effects on herbaceous biomass. Landscape curvature had an additional indirect effect on hotspots through its negative effect on leaf Na; as a result, the standardized total effect of landscape curvature on hotspot probability was −0.49 (Appendix F). While soil fertility had no direct effect on hotspot occurrence, rainfall had a negative direct effect as well as a weak negative indirect effect mediated through its influence on soil fertility and leaf nutrients.

Leaf P, while included in the a priori model, dropped out of the final significant structural equation model. In the context of the final model, herbaceous biomass had negative effects on the three remaining leaf nutrients while soil fertility had positive effects on leaf Na and Mg but not N. Hotspot occurrence was positively associated with the three leaf nutrient concentrations, but the path strength from N was twice as strong as that of Na or Mg. In support of the predator-detection hypothesis, the direct path from herbaceous biomass to hotspot occurrence was negative. As a result of the direct and indirect effects, the total effect of herbaceous biomass on hotspot occurrence (−0.66) was the largest of any variable in the model (Appendix F). As discussed previously, the negative relationship between hotspots and herbaceous biomass was not unexpected given that herbivores reduce standing plant biomass in permanent resident areas through consumption. However, to further explore the potential feedback of this relationship (i.e., Fig. 2), we tested the non-recursive paths between herbaceous biomass and hotspots (i.e., both paths in the model) and an alternative model with identical structure except that only the path from hotspots to biomass was included. In both cases the path from hotspots to biomass was nonsignificant, demonstrating that while hotspots are clearly of lower biomass, not all low-biomass sites across the data set can be explained by the presence of hotspots.

DISCUSSION

Historically, the discussion of the key processes regulating the populations of Serengeti grazers has focused on predation (Sinclair 1985, Sinclair et al. 2003,

Fryxell et al. 2007), forage availability (Sinclair et al. 1985, Mduma et al. 1999), nutrients (McNaughton 1988, Seagle and McNaughton 1992, McNaughton et al. 1997), and energy maximization (Fryxell et al. 2004). This study makes two important contributions toward understanding the factors that determine the habitat distribution of resident Serengeti grazers and ungulate herbivores in general. First, our map results (part 1) show that spatial variation in landscape features influence resource quality and predation risk in ways that correlate with the distribution of Serengeti hotspots. While landscape effects on ungulate nutrient and energy assimilation have long been known (Bell 1970, Seagle and McNaughton 1992), the availability of fine-scale remotely sensed data enables these effects to be extrapolated to entire ecosystems and linked to other processes, such as predation. In Serengeti, lion kill success varies with landscape and habitat features (Appendix B), being lower away from water, vegetated areas, and flat uplands. These separate and combined influences, however, had yet to be investigated with respect to permanent resident areas in a spatially explicit way.

Second, by considering mechanistic processes in a multivariate model (part 2), we were able to simultaneously estimate the relative importance of landscape features, soils, climate, and forage quality and quantity on the occurrence of hotspots, while statistically controlling for their covariation. The model suggested that both resource (bottom-up) and risk factors (top-down) have direct and indirect effects on hotspot occurrence and that the magnitudes of their influences are similar. For example, landscape curvature and distance to rivers had the largest total effects after plant biomass in the model, and even plant biomass is partially correlated with a landscape feature (TWI). In a paper focused on plant mineral nutrition, McNaughton (1988) suggested that the elevated forage quality in hotspots did not preclude the hypothesis that predator protection also contributed to the spatial distribution of resident Serengeti grazers. This multivariate influence could be common for many ungulate populations with natural predators: landscape features create a template of relative risk (Laundre et al. 2001, Ripple and Beschta 2004; Fig. 4) within which more specific permanent habitats are selected based on forage abundance and quality, which are the result of fine-scale influences of climate, soil fertility, habitat features, and herbivore grazing itself (Anderson et al. 2007*b*, de Knegt et al. 2008; Fig. 5).

Evidence for the importance of predation risk

Evidence that the locations of hotspots in Serengeti are influenced by predation risk comes from the direct effects (independent of forage variables) of landscape features on hotspots in the SEM (Fig. 5) and evidence that these features are associated with the spatial distribution of lion kills in Serengeti (Appendix B). In addition to the lion, an ambush predator, the other dominant predator in Serengeti is the hyena, a coursing predator. The effect of coursing predators on hotspots is not known, but the reintroduction of a coursing predator to Yellowstone National Park suggests the influence may be similar: the predation of elk by wolves was modified by classes of landscape features comparable to those identified in our study, specifically, slopes, streams, and forest cover (Kaufmann et al. 2007). The fact that distance to rivers was positively associated with hotspot probability in our results suggests that predation risk is at least equal to water limitation in the determination of the distribution of intermediate-sized resident grazers in Serengeti. Although these residents are obliged to make trips to permanent water sources during the dry season, permanent resident sites occur away from risky, wooded habitats associated with water. Similarly, we suggest that landscape curvature (either highly concave or convex) provides an integrated measure of ungulate risk because it is associated with both opportunities for ambush predators to avoid detection and the degree to which the landscape interferes with the running or acceleration speed of escaping herbivores. Within the context of our model, curved landscapes were negatively associated with hotspot probability but also had a direct negative effect on leaf Na. This is consistent with hydrological and biogeochemical deposition of Na and the distribution of Na-tolerant grasses in Serengeti (Belsky 1986).

The topographic wetness index (TWI) was a significant predictor of hotspots in the map (Appendix D), but had only indirect influence on hotspots in the structural equation model through plant biomass (Fig. 5). This suggests that from an ungulate perspective the main effect of TWI is the presence of tall, poor-quality vegetation. However, this indirect pathway may also be positively associated with predation risk, as the presence of tall vegetation (woody or herbaceous) is associated with increased lion kills (Packer et al. 2005). Similarly, the negative path between biomass and hotspots, even after leaf nutrient concentrations have been taken into account, may also indicate a mechanism for increasing the detection of predators; recall that the reciprocal effect of hotspots on biomass was not significant on its own or in the non-recursive model. In temperate predator–prey systems, the nature of the habitat not only modifies predator–prey encounter rates, but also the outcome of the encounter, with open grassland vegetation being safer from an ungulate perspective (Hebblewhite et al. 2005). We do not mean to imply that forage quantity is not a limiting factor in the population regulation of Serengeti ungulates, because dry-season forage availability limits ungulate survivorship (Mduma et al. 1999). Instead, the model results suggest that the maintenance of short, low-biomass, herbaceous vegetation benefits herbivores through enhanced predator detection as well as increased forage nutritive quality, high rates of primary production, and facilitation of herbivory itself (McNaughton 1984). Moreover, the

path from TWI to biomass suggests that, at least partially, this is a landscape effect.

Forage nutritive quality

The importance of herbivore-generated feedbacks in maintaining the herbaceous vegetation in a protein-rich, sub-mature state has long been known (Vesey-FitzGerald 1960). In Serengeti, the abundance of Na in forage is determined more strongly by the presence of Na-rich grass species in the herbaceous layer than within-species variation in tissue nutrient concentrations (Anderson et al. 2007*b*). Our study suggests that soil and landscape features have important effects on plant Na availability, presumably through their effects on plant species composition. McNaughton (1988) and McNaughton et al. (1997) report no significant difference between soil nutrient concentrations in hotspot and control areas. Similarly, we also found no mean difference between overall soil fertility in hotspots vs. non-hotspot sites (hotspots, 13.9 ± 1.9 [mean ± SE]; non-hotspots, 13.7 ± 1.2; $t_{23} = 0.07$, $P = 0.94$, from a t test assuming unequal variances). In contrast, when the data were analyzed with a more realistic multivariate analysis using SEM, soil fertility emerged as having a positive direct effect on leaf Na and Mg and TWI had indirect influences on Na, Mg, and N through its effects on herbaceous biomass (Fig. 5). Whether these influences are mediated through changes in plant species composition is not known. Either way, landscape features have an important multivariate influence on hotspots from both the standpoint of risk and nutrient availability.

Conclusions and future directions

The idea that herbivores create feedbacks between the vegetation and their own nutrition (Vesey-Fitzgerald 1960, Bell 1970, McNaughton 1984) continues to be a central theme in the literature on savannas dominated by large herbivores (van Langeveld et al. 2003, Archibald et al. 2005, Archibald 2008, Cromsigt and Olff 2008, de Knegt et al. 2008). Ours and other studies (Ripple and Beschta 2004, Kauffman et al. 2007, Riginos and Grace 2008) suggest that the spatial distributions of herbivore concentrations, and thus areas of greatest potential for ungulate-driven feedbacks, are partially determined by behavioral adaptation to risk. One compelling idea in ungulate ecology is that strong top-down influences alter the spatial distribution of herbivores in ways that cascade through the food web, eventually modifying the ecosystem processes on which the upper trophic levels depend (Ripple and Beschta 2004, Frank 2008, Schmitz 2008).

While the theoretical nature of herbivore feedbacks is fairly well-established, there is variation in the types of feedbacks that needs further exploration. Our map suggests a limited number (<30) of Serengeti hotspots, with some (perhaps five) ≥10 km^2 (Fig. 4). The relatively large size of some of these hotspots may facilitate the seasonal shifts in herbivore distribution that have been observed to occur along Serengeti topographic gradients as forage availability changes with season (Bell 1970). Several of the hotspots in our study were measured in the late 1970s by S. McNaughton (1988; *personal communication*), suggesting temporal stability of >30 years. In contrast, studies of grazing lawns in Hluhluwe-iMfolozi Park (HiP) South Africa suggest that they may operate differently. First, the spatial scale of grazing lawns in HiP is smaller, on the order of 10–10 000 m^2 (Cromsigt and Olff 2008). Moreover, grazing lawns in HiP are influenced by interactions among fire, climate, and herbivores, which lead to greater temporal dynamics (Bond et al. 2001, Archibald et al. 2005, Archibald 2008, Cromsigt and Olff 2008). Hotspots in Serengeti, often characterized by grazing lawns (McNaughton and Banyikwa 1995), appear insensitive to such temporal dynamics and are not related to fire in a predictable way (Appendices C and D). So can generalities be found as to what creates and maintains different types of herbivore feedbacks?

Obvious differences exist between the systems, such as the "keystone" role of resident white rhino in HiP (Owen-Smith 1988, Waldram et al. 2008) vs. that of migratory wildebeest in Serengeti (Sinclair et al. 2008). Moreover, average small-scale topographic variation differs between parks, which could potentially alter the scale of feedbacks among soils, vegetation, and herbivores (CV elevation from the DEM: HiP = 0.41; SNP = 0.10). Finally, the density and identity of abundant large predators differs between parks, with HiP dominated by hyenas and Serengeti by lions (Whateley and Brooks 1985, Maddock et al. 1996, Packer et al. 2005), which may change the scale at which herbivores create positive feedbacks. Further comparative research is required to address whether ecological differences between ecosystems contribute to differences between these landscape features or whether hotspots in Serengeti and grazing lawns in HiP are functionally unique.

Finally, we conclude with a question: Why do predators not drive hotspots locally extinct in Serengeti? One explanation could be that the benefit of a consistent and reliable prey base in hotspots is offset by the cost of hunting in areas where prey have greater escape potential. This is compounded by the fact that mixed resident herds are less prone to predation than solitary individuals (Fryxell et al. 2007). Or perhaps hotspots can only flourish in systems in which migrants offer alternative prey at a lower cost and energy investment in hunting. We hope that the increased popularity of meta-analyses and ecosystem comparisons will address questions related to predator regulation of hotspots and the generalities of permanent resident areas in African savannas.

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APPENDIX A

Description of supplementary methods used to study the spatial distribution of Serengeti hotspots (*Ecological Archives* E091-105-A1).

APPENDIX B

Comparison between relative frequency of available habitat and relative frequency of lion kills for three landscape variables (*Ecological Archives* E091-105-A2).

APPENDIX C

Results of the model-building procedure and model assessment against independently collected herbivore abundance data (*Ecological Archives* E091-105-A3).

APPENDIX D

Multiple logistic regression coefficients for the model used to predict the occurrence of Serengeti hotspots (*Ecological Archives* E091-105-A4).

APPENDIX E

Additional maps relevant to the analysis of Serengeti hotspots (*Ecological Archives* E091-105-A5).

APPENDIX F

Table of direct, indirect, and total standardized effects from the Bayesian structural equation model predicting the binomial occurrence of Serengeti hotspots (*Ecological Archives* E091-105-A6).